A NEW KOALA FROM THE PLIOCENE PALANKARINNA FAUNA OF SOUTH AUSTRALIA

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Fig. 1-2

SUMMARY

A new genus and species of koala, *Perikoala palankarinnica* Stirton, is described on part of a left mandible from the Palankarinna fauna east of Lake Eyre in South Australia. The age of the fauna is thought to be early or, possibly, middle Pliocene. Detail features in the teeth have been emphasized. Other than in the koala, *Phascolarctos*, there are suggestions of affinities in the fossil with the bushtail possum, *Trichosurus*, with the giant gliders, *Schoinobates*, and with the ringtailed possums, *Pseudocheirus*. Comparative figures of P_3, M_1, and M_2 in these genera, including the fossil, have been made. Much more fossil evidence is needed to determine the phyletic relationships of the genera studied, and to understand the familial relationships of the koalas to the rather broad family Phalangeridae.

INTRODUCTION

Part of a mandible of a koalalike marsupial was discovered by Mr. Paul F. Lawson in the summer of 1954, when the South Australian members of the 1954 South Australian Museum-University of California expedition were returning from Birdsville to Adelaide. The specimen was found in place about 500 yards south of the Woodard locality where the bulk of the material was located in the escarpment along the west side of Lake Palankarinna. Fragmentary remains of other small vertebrates were found scattered through the matrix at this new site. This is the oldest known record of the Phascolarctinae and is the only one that has been recovered from the Tertiary. The paratype was picked up on the surface by Mr. Richard H. Tedford near this locality in 1953 (Stirton, 1955).

I am grateful to Mr. Herbert M. Hale, Director of the South Australian Museum, for the privilege of describing this interesting new genus. The illustrations were made by Mr. Owen J. Poe, staff artist, in the Museum of Paleontology at the University of California.

Genus **Perikoala** nov.

The characters of this genus are those of the type species until other species are described.

Perikoala palankarinnica sp. nov.

Holotype.—Part of left mandible with talonid of P_3, M_1 and M_2 nearly complete. South Australian Mus. No. P 10893.

Paratype.—Fragment of right maxillary with posterior border of alveolus of P^3, the roots of M^1, M^2 in place but with much of the enamel surface and the inner edge broken away, part of the alveolus of M^3 and the base of the jugal arch. Univ. Calif. Mus. Paleo. No. 45343.

Type Locality.—Greenish-blue, fine grained, sandy gypsiferous clays; flood plain deposit on same level as channel sands of Woodard locality, but about 500 yards farther south; 35 feet above the basal conglomerate. U. C. locality V5375.

"The exposures are along the west side of Lake Palankarinna, east of Lake Eyre; 18 miles S. 75° W. of Etadunna Station homestead. Military grid reference 656431, ordinance sheet Marree, South Australia, H54/1.2.5.6, zones 5 and 6, first edition 1942, scale 1:506880." (Stirton, 1955).

Age.—Early or, possibly, middle Pliocene.

Diagnosis.—Lateral opening of dental canal not discernible on horizontal ramus below M_2.

P_3 with lophid between hypoconid (1) and protoconid interrupted by tiny groove on slope of protoconid; protoconid and small entoconid connected by short high lophid, this continues downward and labiad in wide curve to posterior base of hypoconid enclosing posterior talonid basin which opens posterolabially at that point; outline of talonid rounded, not triangular, without crest continuing from entoconid to posterolabial corner.

M_1 sharply angulate anteromedially; with prominent central basin; paraconid present, separated from much larger metaconid by rather deep lingual valley; metaconid without posterior spur into area of central basin; low irregular transverse crest extends lingually from hypoconid to midline of crown opposite similar crest descending from entoconid.

M_2 divided into anterior trigonid, central, and posterior trigonid basins; vestigial transverse crest between protoconid and metaconid more

(1) The premolar dental terminology is based on apparent analogous positions with those in the molars.

pronounced than one between hypoconid and entoconid; labial part of middle valley not deep transversely nor shelflike.

Anteorbital fossa of maxillary shallow; width of base of jugal arch opposite $M^2 = 6.7$; M^2 as wide as long (in paratype).

Description.—Horizontal ramus below M_2 deeper than in *Trichosurus* but shallower than in *Phascolarctos*, 16.5; thickness below $M_2 = 7.4$; small mental foramen 3.5 in front of anterior root P_3, and below diastemal crest, 1.3 in diameter; surface of bone broken over anterior part of dental canal; lateral opening of dental canal not discernible on horizontal ramus below M_2.

Molars with crenulated enamel surface in occlusal basins; no alveolus for P_2.

Anteroposterior axis of P_3 in line with that of molars; anterior two-thirds of P_3 broken away; evidently bilobed; area back of protoconid preserved; protoconid not occupying anterocentral position; larger than hypoconid; lophid between hypoconid and protoconid interrupted by tiny groove on slope of protoconid; protoconid and small entoconid connected by short high lophid, this continues downward and labiad in wide curve to posterior base of hypoconid enclosing posterior talonid basin that opens posterolabially at that point; outline of talonid rounded, not triangular, without crest continuing from entoconid to posterolingual corner; roots of P_3 larger than on molars, widely divergent.

M_1 partly destroyed on labial side; elongate, sharply angulate anteromedially; paraconid slightly linguad of median position, evidently separated from much larger metaconid by rather deep valley; metaconid with convex lingual surface; lophid extends posterolingually from metaconid to a much lower metastylid (2) on lower median lingual edge of tooth; metaconid without posterior spur into area of central basin; slight crest leads down posteriorly (evidently from protoconid) to median valley where it terminates at transverse commissure adjacent to anterior wing of hypoconid, these wings or crests form labial margin of central basin; entoconid opposite hypoconid; low irregular (due to crenulated anterior and posterior slopes) crest extends lingually from hypoconid to midline of crown opposite similar crest descending from entoconid, this apparent vestigial transverse lophid separates posterior talonid basin from larger central basin; low crest runs from hypoconid posterolingually around to base of

(2) The median lingual stylid present in the molars of *Perikoala*, *Phascolarctos*, *Pseudocheirus* and *Schoinobates* is somewhat analogous in position to the *metastylid* in the Equidae (Osborn and Wortman 1892, Fig. 3). Metastylid in the Equidae is a misnomer since it did not arise from the cingulum nor is it a peripheral cusp. It seems to have arisen from the posterior half of the metaconid but is innervated from the posterior nerve plexus. On the other hand the median lingual stylid in *Perikoala* seems to be peripheral and indeed may have arisen from a cingulum in an ancestral form. I am sure no confusion can arise in referring to this cusp in the koala and related genera as the metastylid.

entoconid ([3]); no hypoconluid; low posterior *entostylid* posterolinguad of entoconid on lingual surface; length of M_1 = 6.4; width across talonid = approximately 3.8 (part of labial surface of hypoconid broken away); roots parallel, more delicate than on P_3, length = 9.5. M_2 nearly rectangular; transverse crests extend from protoconid and metaconid and separate anterior trigonid basin from anterior part of central basin; similar but much less apparent elevations extend from hypoconid and entoconid and divide talonid into shallow posterior talonid basin and posterior part of central basin; no paraconid; enamel surface broken away opposite both protoconid and metaconid; *metastylid* broken away; protoconid opposite metaconid; entoconid slightly anterior to hypoconid, sub-equal, crescentic cusps oriented anteroposteriorly, depth controlled by extensions and positions of anterolingual spur of hypoconid and posterolingual spur of protoconid (this character is intermediate between the features seen in *Trichosurus* and *Phascolarctos*); no anterolabial crest from hypoconid extending down to block mouth of median valley; labial part of median valley not deep transversely nor shelflike; large crenulated central basin; no hypoconulid; *entostylid* as on M_1 well developed on lingual surface below and posterolinguad of entoconid; length of M_2 = 11.5; width across trigonid = 4.3; width across talonid = 4.6; width between hypoconid and entoconid = 2.6; roots as on M_1, length = 8.5.

COMPARATIVE CHARACTERS ON RELATED GENERA

Phascolarctos

1. Mental foramen 2.0 in front of anterior root of P_3, and 2.9 below diastemal crest, 1.7 mm. in diameter.
2. Prominent lateral opening of dental canal below M_3.
3. Small masseteric foramen.
4. Cheekteeth with crenulated enamel surface in occlusal basins.
5. P_1 and P_2 absent.
6. P_3 with slight emargination on lingual and labial sides dividing tooth into anterior and posterior moieties; entoconid equal in size and opposite hypoconid, both connected to larger protoconid by lophids; median crest extends anteriorly from protoconid; connected to smaller

([3]) Osborn and Wortman (1892, p. 89, Fig. 3) first described *entostylid* as a little reinforcing cusp that grew up behind the entoconid. This was labelled on a *Mesocyon* tooth. A month later in another paper ("The history and homologies of the human molar cusps," *Anatomischer Anzeiger*, Jahrg. VII., 8vo, Jena, 740-747.) Osborn referred to the same cuspid as "——the distal or intermediate cusp"—— as——"hypoconulid" and labelled it on a lower molar of *Homo*; furthermore he inferred its presence in *Macis* and *Anaptomorphis*. At first, evidently, Osborn did not recognize the homology of this conulid in the Primates and in the Equidae but in 1918 he labelled the posterior conulid on all equid lower molars and premolars as hypoconulid. Consequently, here, I am referring to the term *entostylid* as the "——little reinforcing cusp that —— appears ——" behind the entoconid.

protoconid by anteroposterior crest; lophid continues from entoconid to posterolingual corner; low concave posterior lophid forming posterior edge of talonid basin; slight posterolingual shelf; no paraconid; roots not widely divergent; position aligned with anteroposterior axis of molar series.

7. M_1 nearly rectangular, not sharply angulate anteromedially; paraconid vestigial and not separated from metaconid by deep lingual valley; paralophid (4) curves around anterior border of tooth to vestigial paraconid; paraconid connected posteriorly to metaconid; protoconid smaller than metaconid; metaconid with nearly flat lingual surface; lophid extends posterolingually from metaconid to vestigial metastylid on median lingual edge of tooth; metaconid with posteromedian spur; protoconid with posterior spur terminating in median valley (homologous with part of labial border of central basin in *Perikoala*); low trenchant ridge connects protoconid with entoconid labially; trigonid and talonid basins instead of central basin; very low but distinct metalophid crosses middle of crenulated basin diagonally where it joins lophid that connects metaconid and metastylid; entoconid opposite hypoconid; no crest extends lingually from hypoconid into talonid valley towards entoconid; talonid valley anteroposterior in direction; low crest runs from hypoconid posterolingually around to entoconid; but no posterior talonid basin is formed; entostylid present; length of $M_1 = 8.0$; width across talonid = 5.0.
8. M_2-M_4 rectangular; trigonid and talonid basins widely open anteroposteriorly; no paraconids; protoconids opposite metaconids; hypoconids opposite entoconids, subequal, crescentic cusps oriented anteroposteriorly; labial shelflike median valleys deep, terminated lingually by anterolingual spurs of hypoconids (metalophids) and posterolingual wings of protoconids (protolophids), points of termination close to midlines of teeth; no indications of transverse crests directly connecting protoconids with metaconids or hypoconids with entoconids; small anterolabial crests of hypoconids that extend down to block mouths of median valleys become progressively stronger from M_2-M_4. Metastylids and entostylids though somewhat inconspicuous become progressively weaker from M_2-M_4.

Pseudocheirus

1. No mental foramen anterior to P_3.
2. One small lateral opening of dental canal below M_1.
3. Tiny masseteric foramen posterior to opening of opening of posterior dental canal.

(4) For lophid terminology see Stirton, 1941, p. 414, Fig. 4

4. Cheekteeth with smooth enamel surface.
5. P_1 and P_2 present; P_2 smaller than P_3.
6. P_3 without lingual and labial emarginations, narrowly triangular; protoconid anterior to and higher than oblique hypoconid crest; hypoconid crest separated from entoconid by commissure; entoconid slightly linguad of hypoconid, in proximity of, but not connected to protoconid by crest; valley between protoconid and entoconid open across tooth; valley between paraconid and protoconid distinct; roots not widely divergent; position aligned with anteroposterior axis of molar series.
7. M_1 sharply angulate and narrower anteromedially; faint indication of paraconid; lingual surface between metaconid and anterior tip depressed as vestigial valley; paralophid descends from protoconid to anterolabial base of tooth; narrow trigonid valley opens anteriorly slightly labiad of midline; protoconid much smaller than metaconid, rather flat shaped cusp; metaconid with flat lingual surface; lophid extends posteriorly from metaconid to vestigial metastylid on median lingual edge of tooth; protoconid with short posterior crest that extends down to edge of labial mouth of long narrow diagonal median valley; prominent metalophid runs diagonally across center of tooth and connects to vestigial metastylid; no central basin; anteroposterior trigonid trench instead of basin; talonid basin; entoconid anterior to hypoconid, not connected; no crest extends lingually from hypoconid into talonid basin toward entoconid; talonid lophids diagonal in direction; sharp diagonal hypolophid extends across to posterolingual corner of tooth to low but distinct hypoconulid; no entostylid; length of $M_1 = 4.1$; width across talonid $= 2.2$.
8. M_2 — M_4 narrow, elongate, angulate anteriorly; trigonid and talonid basins narrow, bounded posteriorly by protolophids and hypolophids with lingual openings between metaconids and metastylids and between entoconids and hypoconulids; on M_1 and M_2, on M_3 and M_4 posterior openings of talonid basins between entoconids and hypoconulids because entostylids are missing; no paraconids; metaconids anterior to protoconids; entoconids anterior to hypoconids, metaconids and entoconids larger than protoconids and hypoconids, protoconids and hypoconids crescentic, metaconids and entoconids trenchant, all four cusps oriented obliquely; both labial and lingual median valleys short, directed anteriorly; no indications of transverse crests connecting protoconids and metaconids, or hypoconids and entoconids; no small crests leading directly anterior from hypoconids.

Schoinobates

1. No mental foramen anterior to P_3.

2. Two and sometimes three lateral openings of dental canal may occur below P_3, M_1 or anterior end of M_2.
3. Small masseteric foramen present.
4. Cheekteeth with smooth enamel surface.
5. P_1 seldom present, greatly reduced; P_2 absent.
6. P_3 larger and with more complicated patterns than in *Pseudocheirus*, faint lingual and labial emarginations, narrow, nearly rectangular; protoconid anterior to and higher than obliquely curved hypoconid crest; hypoconid faintly discernible on crest; hypoconid crest connected to indistinct entoconid; entoconid connected to larger protoconid by curved crest; but posterolingual crest present; posterolingual sloping talonid basin with low ridge at its posterior margin; valley between protoconid and entoconid closed by high sharp crest lingually; distinct valley between paraconid and protoconid closed by crest lingually, position aligned with anteroposterior axis of molar tooth row.
7. M_1 not as sharply angulate and narrow anteromedially as in *Pseudocheirus*; paraconid small but distinct, connected posteriorly to metaconid by sharp lophid; lingual surface between paraconid and metaconid marked by distinct valley; paralophid descends from protoconid to anterolabial base of tooth; trigonid basin wider than in *Pseudocheirus* opens anteriorly slightly labiad of midline; protoconid much smaller than metaconid, slightly less flattened than in *Pseudocheirus*; lophid extends posterolingually from metaconid to median lingual edge of tooth; faint metastylid; metaconid with posterolabial spur; protoconid without posterior crest extending down to edge of labial mouth of diagonal median valley; slight shelflike process at mouth of median valley; prominent metalophid runs diagonally across tooth and connects to spur back of metaconid to a small metastylid; no central basin; entoconid anterior to hypoconid not connected by lophid; no crest extends lingually from hypoconid into talonid valley toward entoconid; talonid basin diagonal in direction; hypolophid interrupted where talonid basin opens posteriorly; no hypoconulid; tiny entostylid posterolingually from entoconid; small conulid posterolabially and at base of entoconid in talonid basin, also present on M_2 but not on M_3 and M_4; length of M_1 = 4.2; width across talonid = 2.5.
8. M_{2-4} narrow, elongate, broadly angulate anteriorly; trigonid and talonid basins relatively narrow but wider than in *Pseudocheirus*; protolophids not continuous through to metastylids, and hypolophids not continuous to posterior lingual corners of teeth; no paraconids; metaconids anterior to protoconids, entoconids anterior to hypoconids, metaconids and entoconids larger than protoconids and hypoconids, protoconids and hypoconids crescentic, metaconids and entoconids trenchant, all

four cusps oriented obliquely; both lingual and labial median valleys short, directed anteriorly; no indications of transverse crests connecting protoconids and metaconids, or hypoconids and entoconids; no small crests leading directly anterior from hypoconids; stylids vestigial or absent and no hypoconulids on M_2, M_3 and M_4.

Trichosurus

1. Mental foramen 1.5 in front of anterior root of P_3 and 2.1 below diastemal crest.
2. Tiny lateral opening of dental canal present or absent below posterior end of M_3.
3. No masseteric foramen.
4. Cheekteeth with smooth enamel surface.
5. P_1 present, P_2 absent.
6. P_3 without lingual and labial emargination, broadly triangular talonid with single median crest; no paraconid; roots not widely divergent; position oblique to anteroposterior axis of molars.
7. M_1 sharply angulate anteriorly; no paraconid; paralophid extends from protoconid straight forward to anterior tip; protoconid in anteromedian position, larger than metaconid; metaconid with convex linqual surface; no posteromedian spur from metaconid and no metastylid; protoconid with prominent lophid running posteriorly into center of tooth where it joins another coming forward from hypoconid blocking transverse central valley; area of central basin open as wide as lingual valley; entoconid opposite hypoconid, connected by transverse lophid; low crest runs from hypoconid posterolingually around to entoconid, forming shallow posterior talonid basin toward lingual side of talonid, no suggestion of hypoconulid on crest below and behind entoconid; length of $M_1 = 6.8$; width across talonid $= 4.5$.
8. M_2 with talonid slightly wider than trigonid, M_3 — M_4 with trigonids wider than talonids; trigonids and talonids traversed by high lophids between protoconids and metaconids, and hypoconids and entoconids; no trigonid, talonid nor central basins; no paraconids; protoconids and hypoconids opposite, crescentric cusps; metaconids and entoconids opposite, semi-crescentic, oriented anteroposteriorly, subequal; labial median valleys not shelflike, terminated lingually at a point labiad to midline of tooth; no ridge leading directly forward from hypoconids down into median valleys; no lingual stylids.

CONCLUSION

Even with the limited evidence available *Perikoala palankarinnica* n. gen. and n. sp. is phascolarctine though the characters show it is

generically distinct from the living koala. If it is directly ancestral to *Phascolarctos* or even in a proximity to that position, considerable evolution has occurred in the group since late Miocene and early Pliocene time.

The patterns in the molars may indicate a distant relationship to a bilophodont marsupial. The koala patterns could have been derived from primitive bilophodont teeth somewhat like that possessed by the ancestors of *Trichosurus*. It is indeed unfortunate that no teeth were found with *Wynyardia* which otherwise shows trichosurine affinities.

Without some fossil evidence it is difficult to even guess where *Pseudocheirus* and *Schoinobates* fit into this phyletic picture. They are as specialized as *Phascolarctos* in their cheekteeth and in a somewhat different direction. Much more evidence is needed from fossils to determine the phyletic relationships of these genera, and to understand the familial relationships of the koalas to the rather broad family Phalangeridae.

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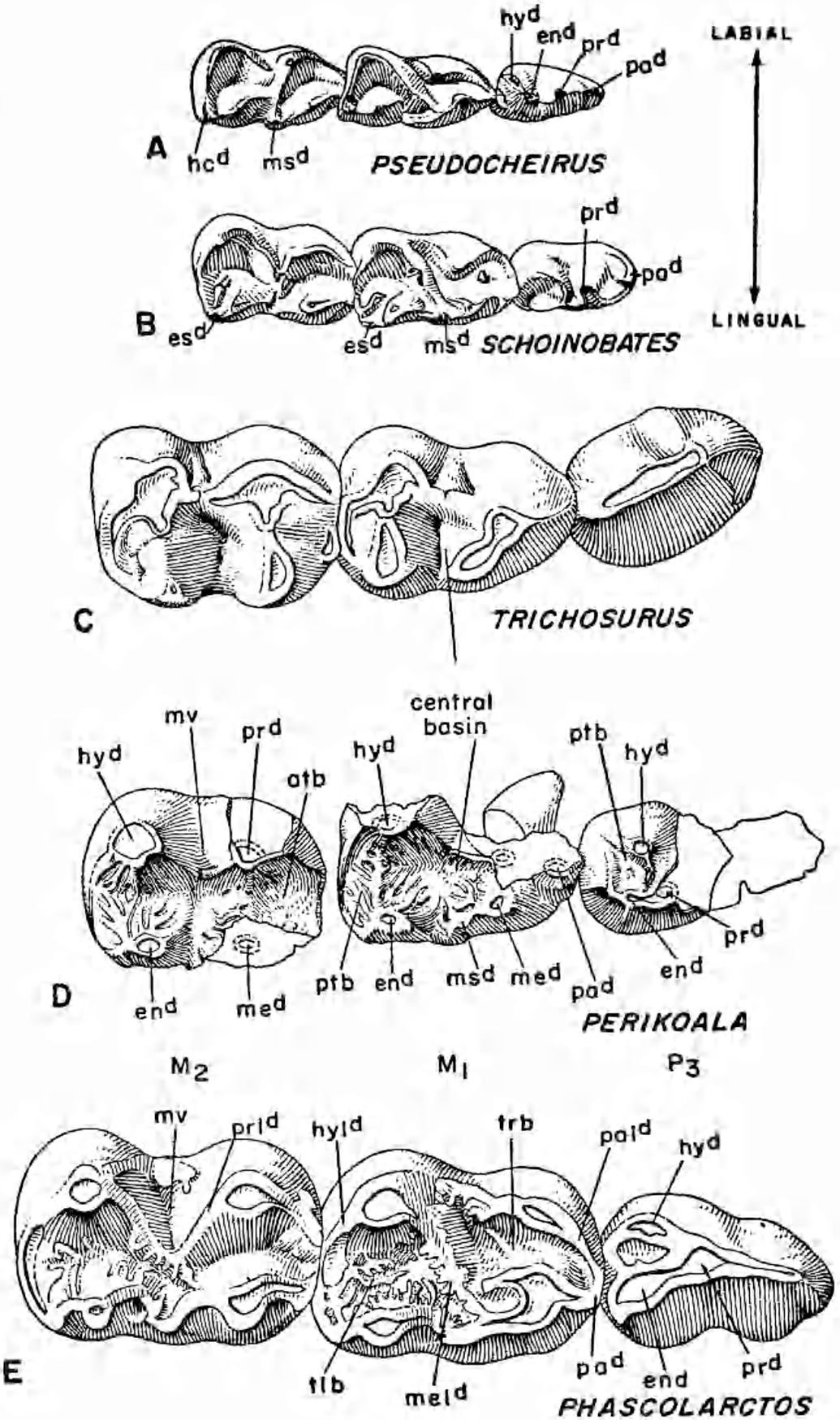

Fig. 1. Comparative occlusal views of left P_3, M_1 and M_2 in *Pseudocheirus lanuginosus*, *Schoinobates volans*, *Trichosurus vulpecula*, *Perikoala palankarinnica*, *gen. et sp. nov.* and *Phascolarctos cinereus* (X5) The anterior face of the trigonid is well worn in *Schoinobates*. *atb*, anterior trigonid basin; *ent*^{d}, entoconid; *est*^{d}, entostylid; *hcd*, hypoconulid; *hyl*^{d}, hypolophid; *hy*^{d}, hypoconid; *med*, metaconid; *mel*^{d}, metalophid; *mst*^{d}, metastylid; *mv*, median valley; *pa*^{d}, paraconid; *pal*^{d}, paralophid; *prd*, protoconid; *prl*^{d}, protolophid; *ptd*, posterior talonid basin; *tlb*, talonid basin; *trb*, trigonid basin.

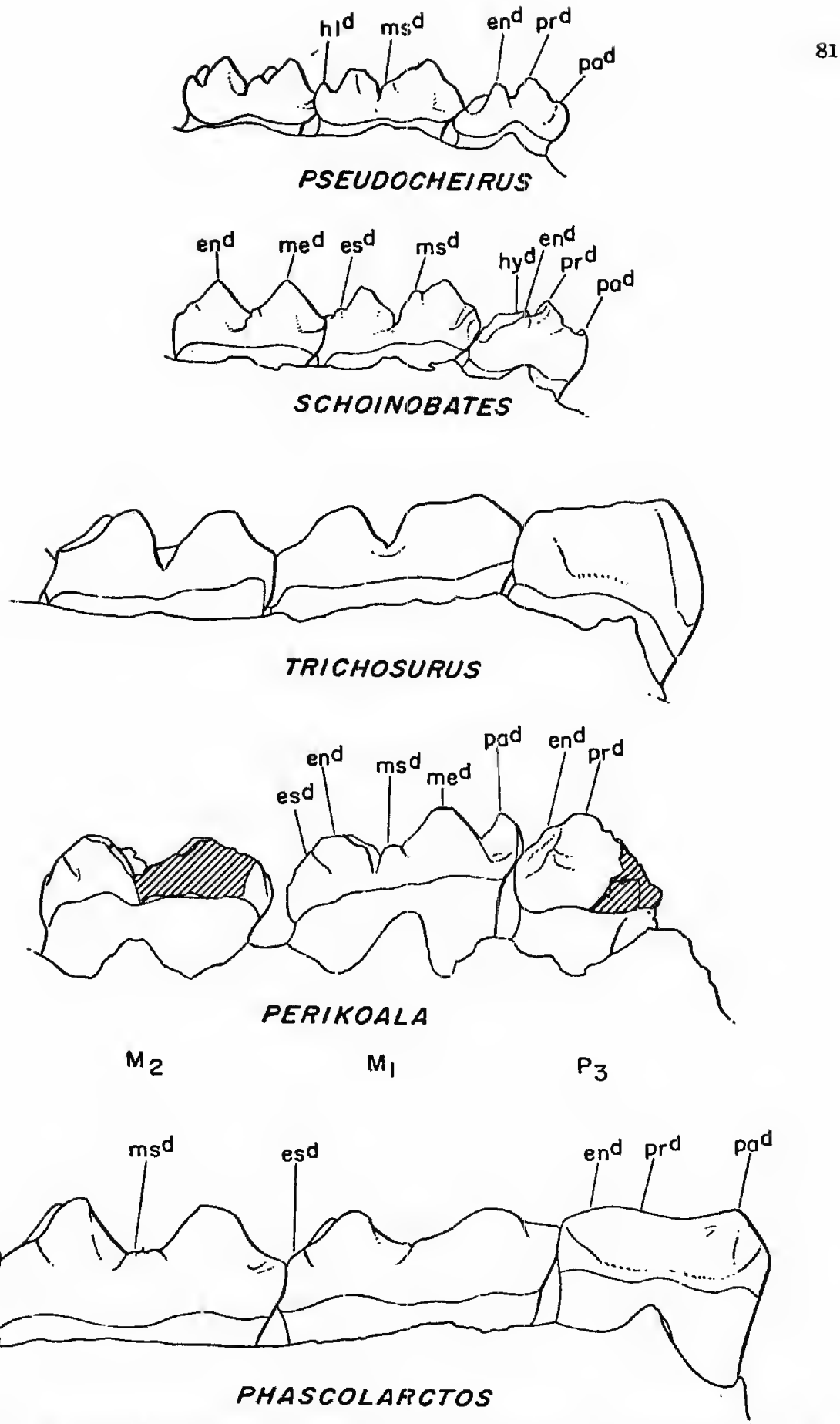

Fig. 2. Comparative lingual views of left P_3, M_1, and M_2 in *Pseudocheirus, Schoinobates, Trichosurus, Perikoala n. gen.*, and *Phascolarctos* (X5).